

PRIONOPSIS (ASTERACEAE: ASTEREA) UNITED WITH GRINDELIA

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ABSTRACT

The monotypic genus *Prionopsis* is distinguished from *Grindelia* only by a difference in the pappus. Studies of morphological variation show that the two taxa are otherwise identical even in micromorphological features, and recent studies of restriction site variation in chloroplast DNA further suggest *Grindelia* without *Prionopsis* is paraphyletic. The proposal is made to enlarge *Grindelia* by including *Prionopsis* as *Grindelia papposa* Nesom & Suh, *nom. nov.*

KEY WORDS: *Prionopsis*, *Grindelia*, *Astereae*, *Asteraceae*

Prionopsis ciliata (Nutt.) Nutt. is a species endemic to the south-central United States. Nuttall originally described it as a member of *Donia* R. Brown (a synonym of *Grindelia* Willd.) but later segregated the species as the monotypic genus *Prionopsis* Nutt. De Candolle regarded the species as a member of *Haplopappus* DC., and Hall maintained it there nearly a century later as the monotypic *Haplopappus* sect. *Prionopsis* (Nutt.) H.M. Hall (see citations below for references).

Several recent floristic treatments of the southeastern to midwestern and western United States (Cronquist 1980; Martin & Hutchins 1981; Barkley 1986) have without comment treated *Prionopsis ciliata* as a member of *Haplopappus*. *Haplopappus* in North America, however, is now dismantled and apportioned among genera of several major clades of *Astereae* (Nesom *et al.* 1990; see Nesom & Morgan 1990 for a summary). In contrast, *Prionopsis* has been maintained as a separate genus by Johnston (1970, p. 1572), who noted that "it is closely related to *Grindelia* to which genus it probably should be

referred." Another Texas botanist had difficulty in distinguishing the two genera, as a photographic guide (Warnock 1974) pictured a plant of *Prionopsis* but identified it as *G. squarrosa* (Pursh) Dunal.

Hall (1928, p. 27) observed that *Grindelia*, "because of its much narrowed and deciduous pappus awns, closely resembles section *Prionopsis*," which he regarded as "doubtfully placed in *Haplopappus*." Steyermark (1937, p. 250) did not find the pappus of *Prionopsis* to be deciduous and rejected a hypothesis of such close relationship between *Prionopsis* and *Grindelia*, although he commented that there was perhaps a "real relationship" between the two in the "reduced number of pappus bristles compared with most of the other sections [of *Haplopappus*]." His comments on the phylogenetic relationships of *Grindelia*, however, were ambiguous, because in the same discussion he concluded that the genus was a member of the tribe Heliantheae, where it represented a "connecting link" to the tribe Astereae. Steyermark's phylogenetic diagram showed *Prionopsis* most closely related to *Xanthisma* DC., but features of the latter do not place it in such a close relationship.

Phylogenetic position of *Prionopsis* and *Grindelia*

Prionopsis and *Grindelia* are integral members of the "*Xanthocephalum* group," which also includes the genera *Xanthocephalum* Willd., *Isocoma* Nutt., *Stephanodoria* E. Greene, and *Olivaea* Schultz-Bip. ex Benth., and the "phyllocephalus group" of *Haplopappus* DC. The plants of these generic-level taxa are characterized by a suite of features that we believe to be homologous and indicative of membership in a monophyletic lineage: yellow ray flowers (if present), disc corollas with the throat abruptly ampliate above the tube, deltate to ovate-lanceolate disc style appendages, and a base chromosome number of $x=6$. For the most part, these taxa have been previously hypothesized to be closely related among themselves (Jackson 1966; Jackson & Dimas 1981; Lane 1983; Lane & Hartman 1985; Hartman 1990). In a broader context, the *Xanthocephalum* group is part of the *Haplopappus* - *Machaeranthera* phylad, essentially as delimited by Morgan & Simpson (1992).

Prionopsis and *Grindelia*

Plants of *Prionopsis* are taprooted annuals with clasping, serrate-spinulose leaves, a glabrous but punctate-resinous herbage, linear-lanceolate phyllaries with spreading apices, ray flowers with yellow, weakly coiling ligules, dimorphic achenes, and pappus bristles that tend to be basally caducous. In this set of features, *Prionopsis* is morphologically indistinguishable from *Grindelia*.

The cells in the throat region of the disc corollas of *Prionopsis* and all species of *Grindelia*, including South American and even the most specialized

North American ones, produce relatively long, straight-sided crystals easily seen in whole mounts of corollas. These crystals are flat, mostly straight at the ends, and they lie at various angles within the cells, where they are mostly about as long as the cell diameter but commonly mixed with fewer, similar but smaller ones. Among the remaining members of the *Haplopappus* - *Machaeranthera* lineage, similar crystals (although smaller and less densely arranged) have been found only in *Xylorhiza* Nutt. and some species of *Hazardia* E. Greene. Among other *Astereae*, such crystals occur only in the goldenaster lineage, where they are diagnostic (Nesom 1991 and an unpublished survey of the tribe). These large, distinctive corolla crystals are a specialization that distinguishes *Grindelia* and *Prionopsis* from their closest relative, *Olivaea*, as well as all other taxa of the *Xanthocephalum* group.

Grindelia, *Prionopsis*, and also *Xanthocephalum* have a tendency to produce turgid, four-angled achenes with thickened walls, a morphology not seen elsewhere in the *Xanthocephalum* group. As observed by Nesom (1990, 1992), however, the species of at least one group of *Grindelia* produce dimorphic achenes, the outer turgid and four-angled, the inner strongly compressed, with numerous, thin nerves on each of the two faces. The same dimorphism also occurs in *Prionopsis*.

Howe (1975) reported that antipodal cells of the female gametophyte of *Prionopsis* and three species of *Grindelia* produce haustorium-like outgrowths. Although such outgrowths apparently are uncommon, they are known from various other genera of North American *Astereae*, but comparative data from other taxa of the *Xanthocephalum* group are not available.

Prionopsis ciliata differs from species of *Grindelia* primarily in its pappus of numerous awn-like bristles connate in a ring at their base. The bristles tend to be persistent, but a basal abscission layer apparently forms on fully mature achenes, where they commonly loosen and detach basally as a unit, or more rarely, in basally united groups. The pappus of *Grindelia* achenes is composed of individual, awn-like bristles similar to those of *Prionopsis*, but they are usually fewer in number, not basally united, and easily caducous, breaking off at the slightest touch. North American species of *Grindelia* produce 2-8 pappus bristles per achene but various South American species usually produce more. *Grindelia bupththalmoides* DC., in particular, typically produces 8-12 bristles per achene, but achenes of some individuals may produce 15 or more bristles (Cabrera 1932). Such a pappus is very similar to that of *Prionopsis*, although the bristles are not basally united.

With its relatively large number of bristles, the pappus of *Prionopsis* at first consideration might appear to be primitive, but it may instead be an atavistic feature, retained in the evolutionary origin of the species, perhaps analogous to the pappus appearing sporadically in some plants of the annual species *Xanthocephalum gymnospermoides* (A. Gray) Benth. The pappus in other species of *Xanthocephalum*, including the remaining annual species (the

closest relatives of *X. gymnospermoides*) is mostly absent or represented by a low corona, sometimes with an erose or toothed margin. The pappus of typical *X. gymnospermoides* is similar, but in scattered populations from Chihuahua (e.g., Lane 2494 [TEX]; Valdes R. 18 [LL]), a ring of 15 to 20 persistent pappus bristles 0.8 to 1.4 mm high rarely occurs. As interpreted here, such a pappus probably represents the vestigial occurrence of the primitive type for the whole *Xanthocephalum* group, such as found in *Isocoma* and the phylogenetic precursors to the *Xanthocephalum* group (Nesom, Suh, & Simpson in prep.). The hypothesis that the pappus of *Prionopsis* is specialized is strengthened by the recognition of *Olivaea* as the sister group to *Grindelia* and *Prionopsis*, since the pappus of *Olivaea* comprises a few, separate, basally caducous bristles nearly identical to those of *Grindelia*.

Wide variation in pappus morphology (presence and absence, variability in the degree of elaboration) is common in many genera throughout various tribes of Asteraceae. Within American Astereae, striking examples can be found within *Townsendia* Hook., *Erigeron* L., *Chaetopappa* DC., and others. Continued recognition of *Prionopsis* as a genus separate from *Grindelia*, based solely on a difference in pappus, is inconsistent with accepted generic concepts across the tribe and family.

Prionopsis as a member of *Grindelia*

Studies in the *Xanthocephalum* group by Suh (1989) of patterns of variation in chloroplast DNA restriction sites show that *Prionopsis* is most closely related to species of *Grindelia* and that *Grindelia* is paraphyletic without the inclusion of *Prionopsis*. In addition to *Prionopsis*, Suh's study has included four species of *Grindelia*. His data strongly suggest that *Prionopsis* is the sister group of *G. microcephala* DC. and *G. adenodonta* (Steyerm.) Nesom; these three species in turn are the sister group of *G. lanceolata* Nutt. and *G. nuda* A. Wood, which form a more weakly supported species pair. Morphological studies (Nesom 1990, 1992) place these four species in a broader taxonomic context.

In view of (1) specialized morphological features shared by *Prionopsis* and *Grindelia*, (2) a weak and inconsistent morphological basis for maintaining *Prionopsis* as a separate genus, and (3) molecular evidence that suggests that *Grindelia* is paraphyletic without *Prionopsis*, the formal proposal is made here to submerge the latter within *Grindelia*, the earlier-named genus (1807 vs. 1841).

***Grindelia papposa* Nesom & Suh, nom. nov.** (not *Grindelia ciliata* Spreng., 1826). BASIONYM: *Donia ciliata* Nutt., J. Acad. Nat. Sci. Philadelphia

2:118. 1821. *Haplopappus ciliatus* (Nutt.) DC., *Prodr.* 5:346. 1836. *Prionopsis ciliata* (Nutt.) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2. 7:329. 1841. [also the publication of *Prionopsis* as a genus]. *Aster ciliatus* (Nutt.) O. Kuntze, *Rev. Gen. Pl.* 1:317. 1891.

Grindelia papposa might be placed in a monotypic section, since no other North American species of the genus has a similar pappus. The molecular data of Suh, however, do not support such a hypothetically isolated position for the species. Until the infra-generic taxonomic structure of the entire genus is better understood, it seems superfluous to create a category for the single species, based on what appears to be a single, autapomorphic feature.

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